LEMMA MICROMORPHOLOGY IN THE ERAGROSTIDEAE (POACEAE)

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ABSTRACT

Scanning electron microscopy was used to examine the lemma micromorphology of 30 genera and 57 species in the tribe Eragrostideae. Results show four silica deposition patterns: 1) cork cell associated with silica cell; 2) cork cell solitary; 3) cork cell with papillae; 4) cork cell not observed. The presence or absence of epidermal papillae, prickle hairs, micro- and macro-hairs is reported. An electron beam x-ray microanalysis indicated a high silica concentration in all structures examined including the cork cells. The distribution of cork cells and silica bodies has taxonomic significance and two subtribes within the tribe are proposed.

Key word: lemma micromorphology, silica deposition patterns, taxonomic significance, Eragrostideae, Poaceae.

RESUMEN

Se examinó la micromorfologia de la lema de 30 géneros y 57 especies de la tribu Eragrostideae mediante microscopía electrónica de barrido. Los resultados muestran cuatro patrones de deposición de silice: 1) célula suberífera asociada con célula silicífera; 2) célula suberífera solitaria; 3) célula suberífera con papila; 4) no se observó célula suberífera. Se reporta la presencia o ausencia de papilas epidérmicas, aguijones, micropelos y macropelos. El microanálisis con haz electrónico de Rayos X indicó una alta concentración de silice en todas las estructuras examinadas, incluyendo las células suberíferas. La distribución de células suberíferas y cuerpos de sílice tiene significado taxonómico y se proponen dos dentro de la tribu.

Palabras clave: micromorfología de la lema, parrones de deposición de silice, significado taxonómico, Eragrostideae, Poaceae.

INTRODUCTION

The Eragrostideae tribe is composed of warm season grasses with a center of distribution in Africa, with extensions to the Indian subcontinent and Australia, and a sizeable incursion into North America (Phillips 1982). In

North America this tribe is best represented in the semiarid southwestern United States and northern Mexico, where it may comprise more than 50 percent of the grass vegetation (Gould and Shaw 1983).

In the United States and Mexico the tribe is represented by approximately 26 genera and 250 species of native and introduces grasses. The largest genera are *Eragrostis*, *Muhlenbergia*, and *Sporobolus*. Whereas, there are two or three genera of medium size, and the rest of the tribe is composed of an unusually large proportion of small, often monotypic, genera.

Members of the Eragrostideae contain paniculate inflorescences that are composed of several racemose or spicate branches, occasionally reduced to a simple spike. Spikelets commonly have 1 to several florets and the reduced florets when present are usually above the perfect ones. Disarticulation is above the glumes except in *Lycurus* and a few species of *Muhlenbergia*. Lemmas are 3-nerved, except in *Sporobolus* and *Calamovilfa*, which have 1-nerved lemmas, and in *Vaseyochloa*, with several-nerved lemmas. Caryopses have a large embryo with a punctiform or ellipsoid hilum, sometimes enclosed within a free pericarp (Phillips 1982; Gould and Shaw 1983).

Renvoize (1983) surveyed the leaf blade anatomy of the tribe and concluded that its genera have adapted to pioneer or harsh habitats. In adapting to such extremes the leaf blade morphology and anatomy have become highly modified.

Micromorphological features of the floral bracts of grasses have been utilized recently as valuable characters that reflects systematic relationships and evolutionary trends. Studies of the lemma micromorphology have been reported by Bjorkman (1960), Hsu (1965), Baum (1971), Clark and Gould (1975), Thomasson (1978a, 1978b, 1980, 1981, 1984, and 1986), Shaw and Smeins (1979), Terrell et al. (1983), Webster and Hatch (1983), Thompson (1983), and Barkworth (1983). Specific studies of silica cell and silica bodies were reported by Terrell and Wergin (1981). In addition silica cells and silica bodies have been recognized as structures of taxonomic significance in the grass family by numerous investigators including Metcalfe (1960), Ellis (1979), Palmer and Tucker (1981), and in other monocotyledons (Stant 1973).

However, few investigations of the lemma micromorphology of the Eragrostideae have been made with the exception of Sanchez (1983, 1984), who examined the epidermis of glumes, lemmas and paleas of *Blephridachne* and *Munroa*, and Peterson (1989), Peterson et al. (1989) who reported on the lemma micromorphology and leaf anatomy for 32 species of annual *Muhlenbergia*. Therefore, our objective was to study epidermal features of the lemma of 30 genera, 57 species, and two varieties of this tribe using scanning electron microscopy. Our specific objective was to document lemma micromorphology and detect different distributions of any epidermal patterns restricted to specific genera. This information would enable further evaluation of the phylogeny of the tribe.

MATERIALS AND METHODS

Lemmas of 57 species representing 30 genera of the Eragrostideae tribe were examined (Table 1) from herbarium specimens (ENCB, TAES, TEX). Specimens were selected to be representative of their respective genera in the Eragrostideae. Although primarily New World genera were examined, a few Old World genera were included. Three or more specimens per species were selected from different localities. All materials were identified using the most current treatments of the tribe available (Gould 1979; Gould and Shaw 1983). Lemmas were removed from the first and second florets of mature spikelets, oriented with the apex at the right, mounted on aluminum stubs with Avery's spot-o-glue to observe the abaxial surface, and then coated with 20 nm of gold palladium in a vacuum evaporator.

TABLE 1. Collectors and localities for the specific specimens studied, analyzed, and photographed with SEM.

Blepharidachne bigelovii (S. Wats.) Hack. — U.S.A. TEXAS. Pecos Co.: *Warnock 46198* (TAES).
Blepharoneuron tricholepis (Torr.) Nash — MEXICO. DURANGO: 8 mi N of Estacion Coyotes, *Breedlove 18855* (TAES).
Calamovilfa gigantea (Nutt.) Scribn. & Merr. — U.S.A. TEXAS. Hutchinson Co.: 8 mi S of Burger, *Gould 14345* (TAES).
Chaboissaea ligulata Fourn. — MEXICO. JALISCO: Ojuelos, *McVaugh 17058* (TAES).
Crypsis niliaca Fig. & DeNot. — U.S.A. CALIFORNIA. Merced Co.: *Crampton 3573* (TAES).
Crypsis schoenoides (L.) Lam. — U.S.A. CALIFORNIA. Sonoma Co.: *Rubtzoff* (TAES).
Dactyloctenium aegyptium (L.) Beauv. — U.S.A. TEXAS. San Patricio Co.: *Schneider 6329* (TAES).
Dasyochloa pulchella (H.B.K.) Willd. ex Rydb. — MEXICO. COAHUILA: Saltillo, *Valdes-R. 1570*, *Hatch et al. 5055a* (TAES). — U.S.A. TEXAS. Presidio Co. *Valdes-R. 1691*(TAES).
Eleusine indica (L.) Gaertn. — MEXICO. CHIAPAS. Tenejape, *Breedlove 14882* (TAES).
Eragrostis ciliaris (L.) R. Br. — U.S.A. FLORIDA: Canal Point, *Silveus 4065* (TAES).
Eragrostis curtipedicellata Buckl. — U.S.A. TEXAS. Archer Co.: *Gould 9776* (TAES).
Eragrostis erosa Scribn. — MEXICO. CHIHUAHUA: Guachochic, *Bye 6934* (TAES).
Eragrostis mexicana (Hornem.) Link — MEXICO. NUEVO LEON: Galeana, *Hatch et al. 4588* (TAES).
Eragrostis superba Peyr. — U.S.A. NEW MEXICO. Dona Ana Co.: *Yelwa 38* (TAES).
Erioneuron avenaceum (H.B.K.) Tateoka — MEXICO. COAHUILA. General Cepeda, *Valdes-R. 1561* (TAES). HIDALGO: 11 mi N Ixmiquilpan, *Gould 9564* (TAES). MEXICO: 1 km N San Juan Teotihuacan, *Rzedowski 17124* (TAES). NUEVO LEON. Galeana, *Hatch et al. 4998* (TAES). SAN LUIS POTOSI: Guadalcazar, *Valdes-R. 1612* (TAES); *Valdes-R. 1635, 1650* (TAES). ZACATECAS: El Tecomote, *Reeder 6292* (ENCB).
E. avenaceum var. *longiglumis* Parodi — ARGENTINA. JUJUY: Tilcara, *Correll et al. A676* (TEX).
E. grandiflorum (Vasey) Tataoka — MEXICO. MEXICO: Puebla, 9 km NW of San Lorenzo, *Davidse 9315* (TAES).
E. nealleyi (Vasey) Tateoka — MEXICO. COAHUILA: Acuna, *Valdes-R. 1246* (TAES), Saltillo, *Valdes-R. 1531, 1559* (TAES), *Hatch et al. 5050* (TAES). DURANGO: Poanas, *Gonzalez 2792* (TAES). NUEVO LEON: Galeana, *Hatch et al. 5002* (TAES), *Tateoka s.n.* (TAES). — U.S.A. TEXAS. Presidio, *Valdes-R. 1689* (TAES).

TABLE 1 continued

E. pilosum (Buckl.) Nash — MEXICO. COAHUILA: Est. Carneros, Saltillo, *Valdes-R. 1502* (TAES). — U.S.A. TEXAS. Travis Co.: Austin, *Valdes-R. 1653* (TAES).
Gouinia virgata (Presl.) Scribn. — MEXICO. SINALOA: 5 mi N of Mazatlan, *Gould 12233* (TAES).
Gymnopogon foliosus (Willd.) Nees — BRAZIL. BAHIA: Galheirao, *Davidse 12145* (TAES).
Leptocarydion vulpiastrum (De Not.) Stapf — KEYNA. Kiboko Res. Sta., *Hatch 4236* (TAES).
Leptochloa dubia (H.B.K.) Nees — MEXICO. COAHUILA: Buenavista, *Gould 6387* (TAES).
Leptochloa uninervia (Presl.) Hitchc. & Chase. — U.S.A. TEXAS. Hidalgo Co.: *Lonard 2731* (TAES).
Lycurus phleoides H.B.K. — MEXICO. COAHUILA: Sierra de Zapaliname, Saltillo, *Hatch et al. 4499* (TAES).
Muhlenbergia emersleyi Vasey — MEXICO. CHIHUAHUA: Chihuahua, *Valdes-R. 144* (TAES).
Muhlenbergia fastigiata (Presl.) Henrard — BOLIVIA. PUNO: Camjata Hacienda, *Tutin 975* (NY).
Muhlenbergia minutissima (Steud.) Swallen — MEXICO. BAJA CALIFORNIA: Sierra San Pedro Martir, *Moran 24653* (TAES).
Muhlenbergia plumbea Scribn. *in* Beal — MEXICO. Tlaxcala; El Carmen, *Sohns 622* (TAES).
Muhlenbergia pungens Thurb. — U.S.A. NEW MEXICO. McKinley Co.: *Morden et al. 860* (TAES).
Munroa squarrosa (Nutt.) Torr. — MEXICO. CHIHUAHUA: 4.1 mi N of Samalayuca, *Hendrickson 7490* (TEX). — U.S.A. TEXAS. Andrews Co.: *Powell 5882* (TAES).
Neeragrostis reptans (Michx.) Nicora — MEXICO. COAHUILA: Sabinas, *Gould 11241* (TAES).
Pereilema ciliatum Fourn. — MEXICO. CHIAPAS: 15 mi S of Ocozocoautla, *Brunken & Perino 314* (TAES).
Pereilema crinitum Presl — MEXICO. CHIAPAS: 36 km E of Tuxtla Gutierrez, *Gould & Hatch 14374* (TAES).
Redfieldia flexuosa (Thurb.) — Vasey U.S.A. NEBRASKA. Minden, *Hapeman* (TAES).
Scleropogon brevifolius Phil. — MEXICO. PUEBLA: 41 km SW of Perote, Ver. *Koch 77211* (TAES).
Sohnsia filifolia (Fourn.) Airy Shaw — MEXICO. SAN LUIS POTOSI: Guadalcazar, *Sohns 1341* (TAES).
Sporobolus airoides (Torr.) Torr. — MEXICO. COAHUILA: 3 mi N of Parras, *Gould 11550* (TAES).
S. asper (Michx.) Kunth var. *asper* — U.S.A. TEXAS. Jack Co.: *Gould 10286* (TAES).
S. clandestinus (Biehler) Hitchc. var. *canovirens* (Nash) Shinners — U.S.A. TEXAS. Robertson Co.: *Gould 11047* (TAES).
S. cryptandrus (Torr.) Gray — MEXICO. COAHUILA: Piedras Negras, *Gould 11283* (TAES).
S. indicus (L.) R. Br. — MEXICO. JALISCO: 2 mi W of Ayo el Chico, *McVaugh 17206* (TAES).
S. giganteus Nash — U.S.A. TEXAS. Bailey Co.: 2 mi E of Muleshoe, *Gould 7747* (TAES).
S. neglectus Nash — U.S.A. MISSOURI. Barton Co.: *Riggins 723* (TAES).
S. ozarkanus — Fern. U.S.A. MISSOURI. Jefferson Co.: *Riggins 444* (TAES).
S. pyramidatus (Lam.) Hitchc. — MEXICO. MEXICO: Ecatepec, *Rzedowski 20235* (TAES).
Tricboneura elegans Swallen — U.S.A. TEXAS. Cameron Co.: *Lonard 3183* (TAES).
Tridens albescens (Vasey) Woot. & Standl. — MEXICO. NUEVO LEON: Montemorelos, *Gould 12860* (TAES).
T. congestus (L.H. Dewey) Nash — U.S.A. TEXAS. San Patricio Co.: Sinton, *Hatch 4125*, (TAES).
T. muticus (Torr.) Nash — MEXICO. CHIHUAHUA: Ojinaga, *Valdes-R. 719* (TAES).
T. muticus var. *elongatus* (Buckl.) Shinners — U.S.A. TEXAS. Young Co.: *Gould s.n.* (TAES).
T. strictus (Nutt.) Nash — U.S.A. TEXAS. Kenedy Co.: *Johnson 1357* (TAES).
T. texanus (S. Wats.) Nash — MEXICO. NUEVO LEON: Monterrey, *Valdes-R. 1497* (TAES).
Trinochloa stipoides (H.B.K.) Hitchc. — MEXICO. MEXICO: Juchitepec, *Rzedowski 32623* (TAES).
Triodia irritans R. Br. var. *laxispicata* N.T. Burbidge — AUSTRALIA. BALRANALD N.S.W.. *Henderson 333* (TAES).
T. mitchelli Benth. — AUSTRALIA. QUEENSLAND: *Scarth-Johnson 15* (TAES).
T. pungens R. Br. — AUSTRALIA. QUEENSLAND: *Hubbard 7358* (TAES).
Triplasis purpurea (Walt.) Chapm. — U.S.A. TEXAS. 2.5 mi NE of Kenedy Co.: *J. C. Johnson 1357* (TAES).
Tripogon spicatus (Nees) Ekman — MEXICO. VERACRUZ: XALAPA, *Beetle M2218* (TAES).
Vaseyochloa multinervosa (Vasey) Hitchc. — U.S.A. TEXAS. Brooks Co.: *Johnston 54508* (TAES).

Samples were examined at 5 – 15 kV with 0° tilt on a JEOL JSM-25 SII scanning electron microscope. Lemmas of selected genera were examined with electron beam x-ray microanalysis on the JEOL JSM-35 scanning electron microscope to determine the elemental content of specific structures.

To examine the effects of herbarium preservation techniques on specimens, lemmas from living plants (*Tridens*) were fixed in 2.5% glutaraldehyde buffered in 0.1M sodium cacodylate for one hour; washed three times in 0.1M sodium cacodylate buffer for 10 min.; post fixed in 1% osmium tetroxide for one hour; washed three times for 10 min. each time with 0.1M sodium cacodylate buffer; dehydrated in a graded series of ethanol; dried in a DCP-1 critical point drying apparatus; and coated with TV tube koat and 20 nm of gold palladium. Lemmas of several genera were cleaned in xylene in an ultrasonic cleaner for one hour to remove epicuticular wax.

RESULTS AND DISCUSSION

The micromorphological surface features of the lemma of the Eragrostideae exhibit typical "chloridoid" characteristics (Prat et Vignal 1968), such as papillae, microhairs, macrohairs, abundant prickle hairs, and silica cells. This corresponds with the conclusion reported by Renvoize (1983) in the anatomical survey of the leaf blade of this tribe. Unique silica deposition was observed in cork cells (Figs. 1 – 2). An electron beam x-ray microanalysis of this structure indicated a high concentration of silica. The analysis of the cork cell for *Erioneuron avenaceum* (Fig. 3) shows that a high silica concentration is associated with some artifacts of sample preparation (gold & palladium), and electrons emitted from the surrounding environment within the microscope (copper).

For comparative purposes, since all the samples were obtained from dried herbarium specimens, fresh lemma material from *Tridens strictus* was analyzed (Fig. 4). The osmium concentration was remarkably high due to the osmium tetroxide used in specimen fixation. The analyses of the prickle hairs and the silica cell (Figs. 5 – 6) from the same *Erioneuron avenaceum* specimen used for the cork cell analysis, shows a high silica concentration.

The presence or absence of the cork cell, silica cell, papillae, prickle hairs, microhairs, and macrohairs indicate four distinctive patterns within the tribe. The four patterns are discussed with representative examples.

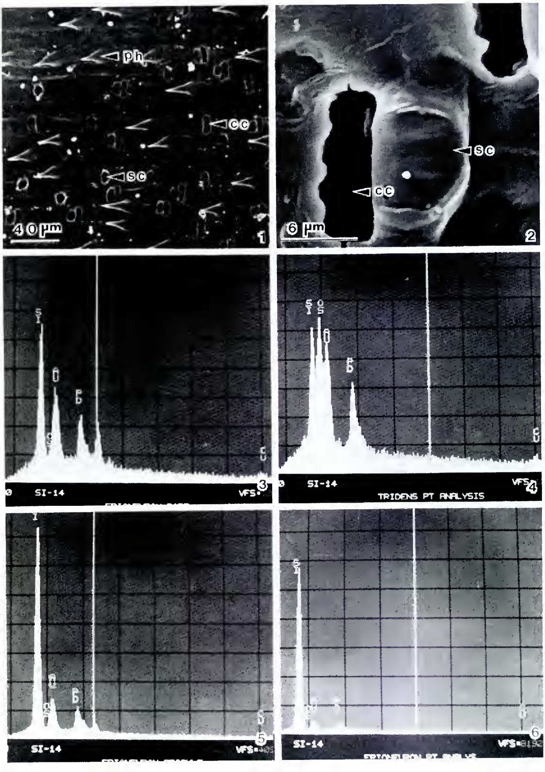
1. **Cork cell associated with silica cell.** In Figure 7 the cork cell is evident with the associated round silica cell in *Triodia irritans* var. *laxispicata*. In *Triodia pungens* and *Neeragrostis reptans*, relatively short dumbbell-shaped silica cells and the associated cork cell are shown (Figs. 8 – 9). Kidney-shaped silica cells and associated cork cell are evident in *Eragrostis*

erosa and *E. mexicana* (Figs. 10 – 11). The cork cell, dumbbell-shaped silica cell, and prickle hairs of *E. ciliaris* (Fig. 12) exhibit a similar pattern reported by Baum (1971) in lemmas of *Avena*, and Terrell and Wergin (1981) in *Zizania*.

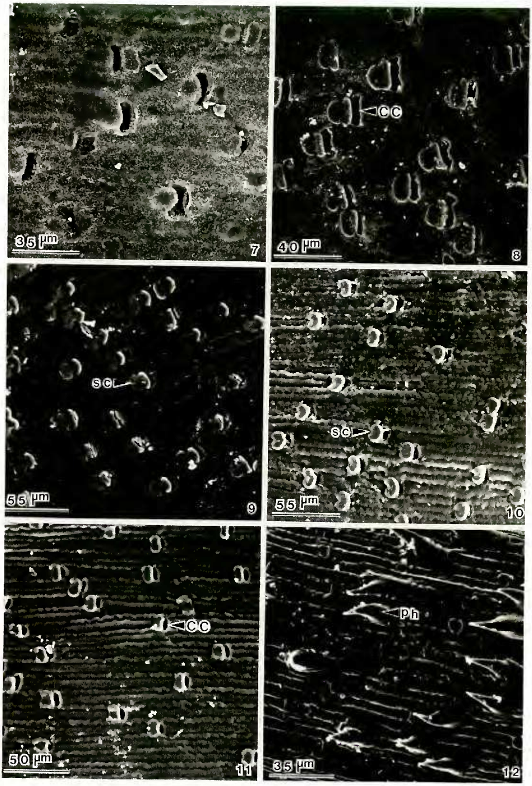
II. **Cork cells solitary**. This pattern characterized a number of the genera observed. In five species of *Tridens* the shape of the cork cell varies from crescent or kidney- to flattened dumbbell-shaped (Figs. 13 – 17). *Triplasis* (Fig. 18), *Sohnsia* (Fig. 19), *Eleusine* (Fig. 20), and *Dactyloctenium* (Fig. 21) have silica cells in rows that are not associated with the cork cells.

III. **Cork cells papillate**. In these taxa the cork cell is associated with small rounded papillae, similar to the ones illustrated by Clark and Gould (1975), Thomasson (1978b), and Terrell and Wergin (1981). This pattern is seen in *Leptochloa* (Fig. 22), *Tripogon* (Fig. 23), *Leptocarydion* (Fig. 24), *Gymnopogon* (Fig. 25), *Trichoneura* (Fig. 26), *Vaseyochloa* (Fig. 27), and *Scleropogon* (Fig. 28). When a silica cell was observed it was associated with the cork cell and papillae. In *Gouinia* a cork cell and papillae are shown but prickle hairs are not abundant (Fig. 29). *Erioneuron* seems to be intermediate between pattern I and II, since the cork cell may or may not be associated with the silica cell (Figs. 31 – 34). The shape of the cork cell was characteristically elongated vertically in *Erioneuron*, with an outline varying between oblong to crenate or scalloped. An abundance of prickle hairs occurs along the epidermal lemmatae.

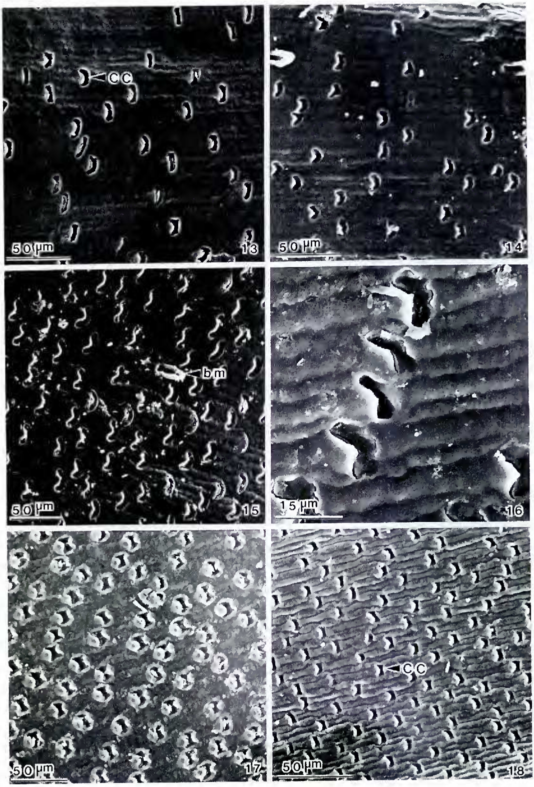
IV. **Cork cells not observed**. This patterms was found in *Munroa* (Figs. 35 – 36). The microhairs observed were hemispheric and similar to those reported by Sanchez (1984). Similar microhairs were also present in the genus *Erioneuron*. Papillae were also evident and abundant. *Blepharidachne* and *Redfieldia* have abundant prickle hairs throughout the epidermis (Figs. 37 – 38). Abundant prickle hairs have been reported for *Blepharidachne* by Sanchez (1983). In *Pereilema* the prickle hairs are associated with papillae over long cells (Figs. 39 – 40). However, a clear distinction could be made based on the long cell's shape. *Pereilema ciliatum* has characteristic raised cell walls forming a ridge around the long cells. In *Triniochloa* papillae, prickles and pitted long cells are shown (Fig. 41). Macrohairs and an abundance of small hooks are seen in *Sporobolus ozarkanus* (Fig. 42). *Blepharoneuron tricholepis* and *Muhlenbergia emersleyi* have bicellular microhairs, prickle hairs, papillae, and deeply undulating long-cells margins (Figs. 43 – 44). This characteristic shape of long cells is also observed in *Chaboissaea* (Fig. 45), *Lycurus phleoides* (Fig. 46), *Muhlenbergia minutissima* (Fig. 47), and *M. fastigiata* (Fig. 48). Dumbbell-shaped silica cells with a relatively wide central portion are seen in *M. plumbea* (Fig. 49), *Sporobolus pyramidatus* (Fig. 50), *S. airoides* (Fig. 51), *S. asper* (Fig. 52), *S. cryptandrus* (Fig. 53), and *Crypsis* (Fig. 54).



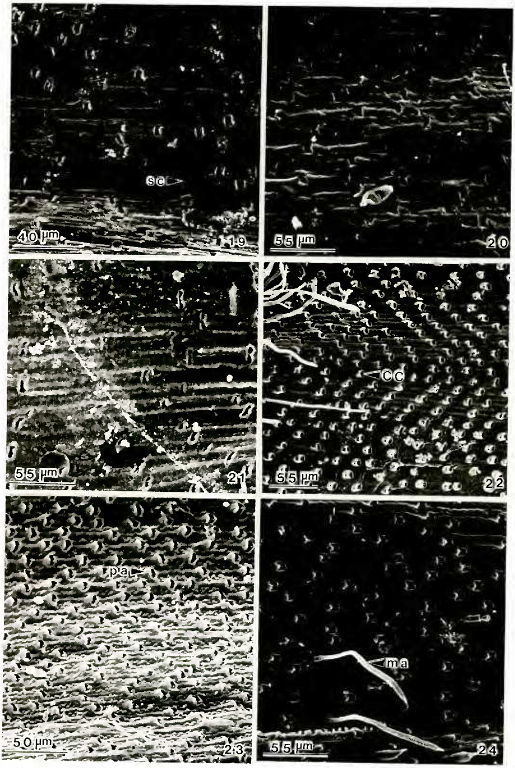
FIGS. 1 – 6. Lemma micromorphology and graphs of electron beam x-ray microanalysis of *Erioneuron* and *Tridens*. Note that a high silica concentration was found for all srructures analyzed. Fig. 1. Silica bodies *E. nealleyi* (*Tateoka s.n.*). Fig. 2. Closeup of silica cell and associated cork cell. Fig. 3. Electron beam x-ray microanalysis of the cork cell of *E. avenaceum* (*Reeder 6292*). Fig. 4. Electron beam x-ray microanalysis of cork cell of *Tridens strictus* (*Valdes-R. s.n.*) Fig. 5. Electron beam x-ray microanalysis of prickle hair. Fig. 6. Silica cell of *E. avenaceum* (*Reeder 6292*). Au = gold; Cu = copper; Us = osmium; Pd = palladium, ph = prickle hair; sc = silica cell, cc = cork cell; SI = silica.



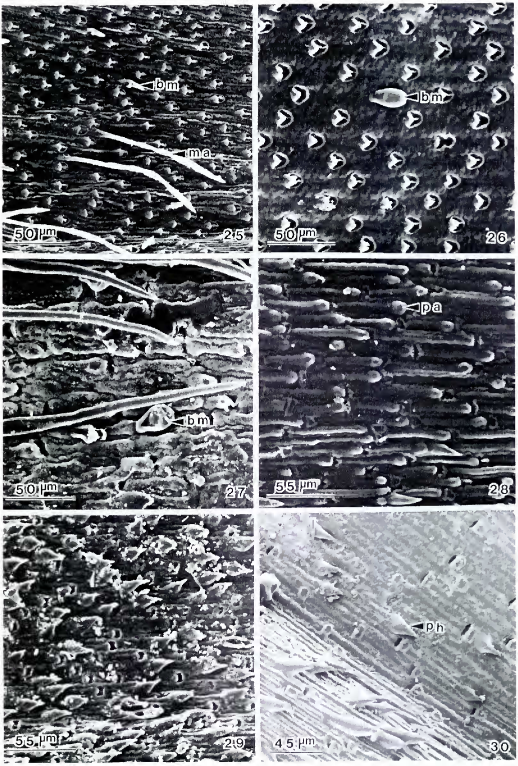
FIGS. 7 – 12. SEM photomicrographs of lemma surfaces from selected genera of Eragrostideae. Note that the silica cells vary from short dumbbell- to kidney-shaped and are associated with a cork cell. Fig. 7. *Triodia irritans* var. *laxispicata* (*Henderson 333*). Fig. 8. *T. pungens* (*Hubbard 7358*). Fig. 9. *Neeragrostis reptans* (*Gould 11241*). Fig. 10. *Eragrostis erosa* (*Bye 6936*). Fig. 11. *E. mexicana* (*Hatch et al. 4588*). Fig. 12. *E. ciliaris* (*Silveus 4065*). SC = silica cell; cc = cork cell; ph = prickle hair.



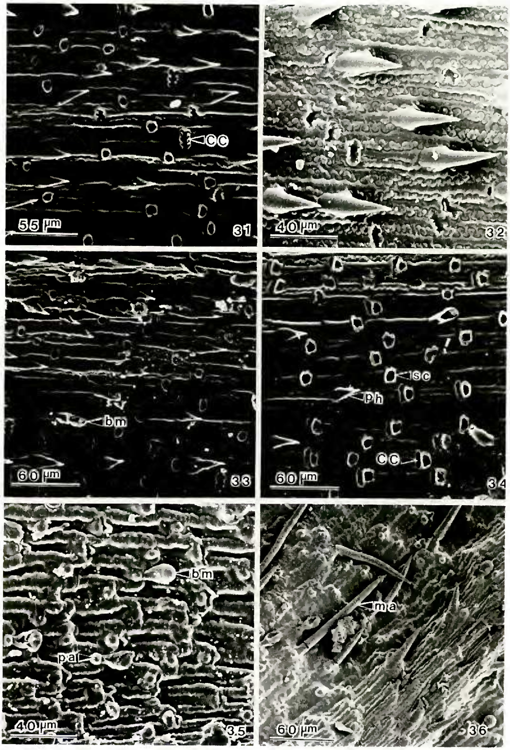
FIGS. 13 – 18. Lemma epidermal patterns for *Tridens* and *Triplasis*. The shape of the cork cell is kidney- to flattened dumbbell-shaped. The bullet-shaped bicellular microhair is characteristic of the genus *Tridens*. Fig. 13. *Tridens albescens* (*Gould 12869*). Fig. 14. *T. texanus* (*Valdes-R. 1497*). Fig. 15. *T. congestus* (*Hatch 4125*). Fig. 16. *T. strictus* (*Valdes-R. s.n.*). Fig. 17. *T. muticus* var. *elongatus* (*Gould s.n.*). Fig. 18. *Triplasis purpurea* (*Johnson 1357*). bm = bicellular microhair; cc = cork cell.



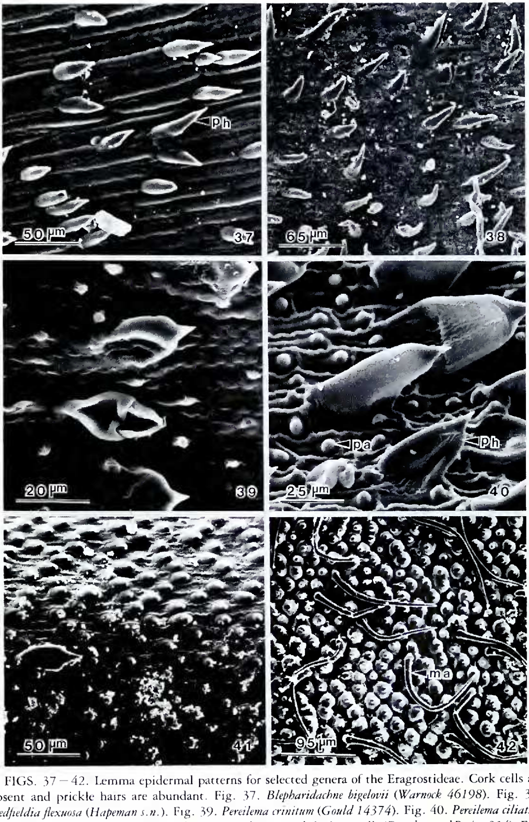
FIGS. 19–24. Lemma epidermal patterns for selected genera of Eragrostideae. Note the small papillae associated with the cork cell and the slender, villous macrohairs. Fig. 19. *Sohnsia filifolia* (*Sohns 1341*) with silica cells in rows and not associated with a cork cell. Fig. 20. *Eleusine indica* (*Breedlove 14882*). Fig. 21. *Dactyloctenium aegyptium* (*Schneider 6329*). Fig. 22. *Leptochloa uninervia* (*Lonard 2731*). Fig. 23. *Tripogon spicatus* (*Beetle M-2218*). Fig. 24. *Leptocarydion vulpiastrum* (*Hatch 4236*). sc = silica cell, cc = cork cell, pa = papillae; ma = macrohair.



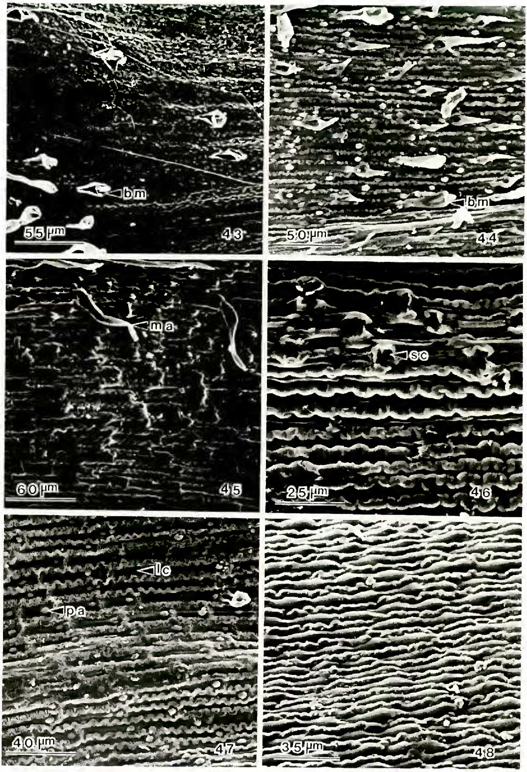
FIGS. 25 – 30. Lemma epidermal patterns for selected genera of Eragrostideae. Note the small papillae associated with the cork cell, the slender villous macrohairs, and hemispheric bicellular microhairs. Prickle hairs are present on *Gouinia* and *Erioneuron*. Fig. 25. *Gymnopogon foliosus* (*Davidse 12145*). Fig. 26. *Tricboneura elegans* (*Lonard 3183*). Fig. 27. *Vaseyochloa multinervosa* (*Johnston 54508*). Fig. 28. *Scleropogon brevifolius* (*Koch 17211*). Fig. 29. *Gouinia virgata* (*Gould 12233*). Fig. 30. *Erioneuron pilosum* (*Valdes-R. 1653*) bm = bicellular microhair, ma = macrohair, pa = papillae, ph = prickle hair.



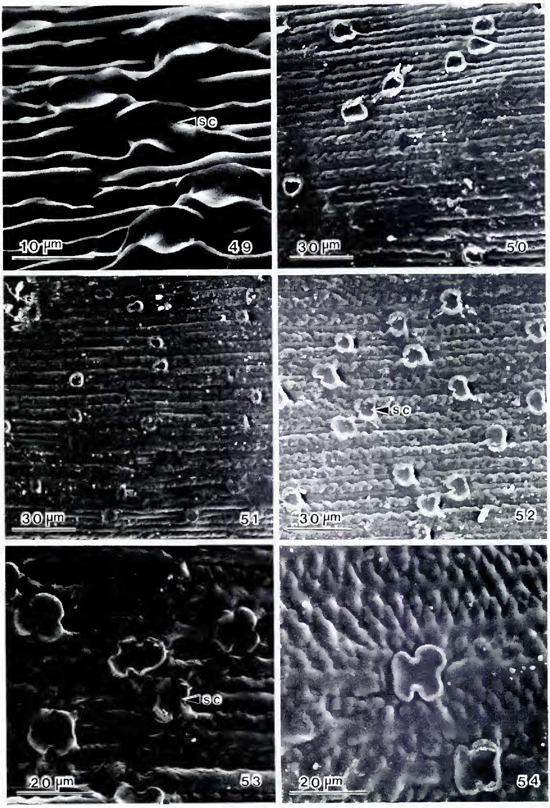
FIGS. 31–36. Lemma epidermal patterns for selected genera of the Eragrostideae. The cork cell shape is oblong to crenate in *Erioneuron* and *Dasyochloa*, with an abundance of prickle hairs. *Munroa* has hemispheric bicellular microhairs and an abundance of papillae. Fig. 31. *Erioneuron nealleyi* (*Valdes-R. 5002*). Fig. 32. *Dasyochloa pulchella* (*Valdes-R. 1691*). Fig. 33. *Erioneuron grandiflorum* (*Davidse 9315*). Fig. 34. *E. avenaceum* (*Valdes-R. 1635*). Fig. 35. *Munroa squarrosa* (*Henrickson 7490*). Fig. 36. *M. squarrosa* (*Rowell 5882*). cc = cork cell; ph = prickle hair; sc = silica cell; bm = bicellular microhair; ma = macrohair; pa = papillae.



FIGS. 37 – 42. Lemma epidermal patterns for selected genera of the Eragrostideae. Cork cells are absent and prickle hairs are abundant. Fig. 37. *Blepharidachne bigelovii* (*Warnock 46198*). Fig. 38. *Redfieldia flexuosa* (*Hapeman s.n.*). Fig. 39. *Pereilema crinitum* (*Gould 14374*). Fig. 40. *Pereilema ciliatum* with characteristic raised cell walls forming a ridge around the long cells (*Brunken and Perino 314*). Fig. 41. *Triniochloa stipoides* (*Rzedowski 20235*). Fig. 42. *Sporobolus ozarkanus* with unique abundant small hooks on the long cells, (*Riggins 444*). ph = prickle hair, pa = papillae; ma = macrohair.



FIGS. 43–48. Lemma epidermal patterns for selected genera of the Eragrostideae. Cork cells are absent and prickle hairs common. Long cells are deeply undulating with one papillae per cell that is located distally. Fig. 43. *Blepharoneuron tricholepis* (*Breedlove 18855*). Fig. 44. *Muhlenbergia emersleyi* (*Valdes-R. 144*). Fig. 45. *Chaboissaea ligulata* (*McVaugh 17058*). Fig. 46. *Lycurus phleoides* (*Hatch et al. 4499*). Fig. 47. *Muhlenbergia minutissima* (*Moran 24153*). Fig. 48. *M. fastigiata* (*Tutin 975*). bm = bicellular microhair; ma = macrohair; lc = long cell; pa = papillae; sc = silica cell.



FIGS. 49 – 54. Lemma epidermal patterns of *Sporobolus* and *Crypsis*. Silica cells are dumbbell-shaped Fig. 49. *Muhlenbergia plumbea* (*Sohns* 622). Fig. 50. *Sporobolus pyramidatus* (*Rzedowski* 20235). Fig. 51. *S. airoides* (*Gould* 11550). Fig. 52. *S. asper* (*Gould* 10286). Fig. 53. *S. cryptandrus* (*Gould* 11283). Fig. 54. *Crypsis niliaca* (*Crampton* 3573). sc = silica cell.

A summary of the epidermal features with high silica content is presented in Table 2. Differences in the patterns of silica deposition are evident. The results of the SEM micromorphological study of the lemma are consistent with those of the anatomical and epidermal features of the leaf blade for the members of the Eragrostideae as reported by Metcalfe (1960), Clifford and Watson (1977), Ellis (1979), Palmer and Tucker (1981), Renvoize (1983), Peterson (1989), and Peterson et al. (1989). *Scleropogon* is the only genus possessing all characters observed.

TABLE 2. Presence (+) or absence (-) of epidermal features on the lemma of Eragrostideae grasses.

GENERA*	CHARACTER				
	Cork cell	Silica cell	Papillae	Prickle hairs	Long cells strongly sinuous with one papillae
Blepharidachne	-	-	-	+	-
Blepharoneuron	-	-	+	-	+
Calamovilfa	-	+	-	-	-
Chaboissaea	-	-	+	-	+
Crypsis	-	+	-	-	-
Dactyloctenium	+	-	-	-	-
Dasyochloa	+	+	-	+	-
Eleusine	+	+	+	+	-
Eragrostis	+	+	-	+	-
Erioneuron	+	+	-	+	-
Gouinia	+	-	+	+	-
Gymnopogon	+	-	+	-	-
Leptocarydion	+	+	+	+	-
Leptochloa	+	-	+	-	-
Lycurus	-	+	-	-	-
Muhlenbergia	-	+	+	+	+
Munroa	-	-	+	+	+
Neeragrostis	+	+	-	-	-
Pereilema	-	-	+	+	+
Redfieldia	-	-	-	+	-
Scleropogon	+	+	+	+	+
Sohnsia	+	+	-	-	-
Sporobolus	-	+	+	-	+
Trichoneura	+	-	-	-	-
Tridens	+	-	-	-	-
Triniochloa	-	-	+	+	+
Triodia	+	+	+	-	-
Triplasis	+	-	-	-	-
Tripogon	+	-	+	-	-
Vaseyochloa	+	-	+	-	-

*Genera are alphabetical.

Phillips (1982) presented a numerical analysis of the tribe dividing the tribe into five groups based on gross morphology. The patterns of silica deposition reported here, correlate in part with that classification based on numerical analysis of morphological features. *Tridens, Triplasis, Erioneuron, Munroa, Leptocarydion, Leptochloa*, and *Tripogon* are placed in group A. The group is characterized as having lemmas with hairy nerves and frequently 2-toothed mucronate or awned apices. All taxa in this group have similar silica deposition patterns except *Erioneuron* and *Munroa*, which are distinct from the other morphologically closely related genera.

Nicora (1962) segregated *Neeragrostis* from *Eragrostis* based upon the extremely long bicellular microhairs of the former. The silica bodies of *Neeragrostis* are dumbbell-shaped and the elongated bicellular microhairs are due to a longer proximal cell. In this study both genera have similar epidermal features, which corresponds to the conclusions of Koch (1978). Koch examined *Eragrostis* in the southeastern United States and reported that *E. hypnoides* (Lam.) B.S.P. also has longer proximal cells in the bicellular microhairs.

Blepharoneuron, Chaboissaea, Lycurus, Muhlenbergia, Sporobolus, and *Crypsis*, a morphologically closely related group (Gould 1979), characteristically lack the cork cells. Clayton and Renvoize (1986) segregate *Muhlenbergia* and *Sporobolus* into the Sporobolinae subtribe using morphological characteristics. Although Clayton et al. (1974) earlier reported Sporoboleae as a tribe somewhat artificial because of the small differences between *Sporobolus* and certain species of *Eragrostis*. Campbell (1985) differed in placement of the genera and included them in the Cynodonteae tribe.

As a result of the examination of the lemma micromorphology a realignment of the genera within the two subtribes is proposed consisting of 1) a subtribe Sporobolinae with *Sporobolus, Muhlenbergia, Chaboissaea, Lycurus, Blepharoneuron*, and *Crypsis* and 2) a subtribe Eleusinae with *Tridens, Triplasis, Erioneuron, Dasyochloa, Munroa, Leptocarydion, Leptochloa*, and *Tripogon*. These two subtribes are not in agreement with the most recent classification (Clayton & Renvoize, 1986) where *Blepharoneuron* is placed in the Eleusinae and not in the Sporobolinae along with *Chaboissaea, Crypsis, Lycurus, Muhlenbergia, Pereilema*, and *Sporobolus*. Campbell (1985) on the other hand recognized a broadly defined tribe (Cynodonteae) that contains all of the genera proposed for this study. The results reported here indicate relationships of the subtribes within this subfamily. However, we recognize the need to correlate these data with gross morphology, as well as molecular, anatomical, and cytological characters to provide useful information in delimiting tribes and resolving taxonomic problems within the Eragrostideae.

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